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PREDATORY BEHAVIOR OF SPITTING SPIDERS (ARANEAE: SCYTODIDAE) AND THE EVOLUTION OF PREY WRAPPING¹

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ABSTRACT

The predatory behavior of the spitting spider *Scytodes* sp. was studied in the laboratory, and an ethogram of the predatory behavior was developed. The principal components usually occur in the order: tapping, spitting, biting, wrapping, feeding. Spitting results in a pair of sticky, zig-zag, transverse bands which pin the prey to the substrate. At the capture site scytodids wrap the prey using the typical form seen in the "higher" spiders: the spider holds the prey in both third legs and alternates the use of right and left fourth legs in applying silk. Prey are eaten at the capture site.

A comparison of prey wrapping by spiders in primitive aerial-web building species with that used by typically "vagrant" species which forage on elevated substrates shows two very different forms of prey wrapping. We argue that prey wrapping at the capture site is an early adaptation of spider radiation into the aerial niche based on the presence of one form or the other in most taxa foraging above ground. Further, the extreme similarity of form of prey wrapping in "higher" spiders which build aerial webs is indicative of a stronger selective pressure for efficient prey handling than for actual prey capture behavior or web geometry.

INTRODUCTION

Spiders of the genus *Scytodes* (Latreille) have the curious behavior of ejecting a mucilagenous glue from the chelicerae at their prey during attack (Monterosso 1927, 1928, Kovoov and Zylberberg 1972) or at predators in self-defense (McAlister 1960, Gilbert and Rayor 1983). Although these spiders are considered primitive on the basis of web structure and several morphological characters (Lehtinen 1967), several aspects of their use of silk during predatory behavior are analogous with those of aerial-web building spider taxa with more advanced characteristics. We examined these behaviors in an undescribed species of *Scytodes* in order to make inferences about the evolutionary stages in the transition from ground-dwelling to aerial-web weaving.

The evolution of web-building spiders from primitive vagrant ancestors to species using silken aerial webs has been the focus of many studies (Kaston 1964,

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1966, Robinson 1975). It is generally agreed that early aerial webs were derived from an accumulation of draglines around the spider's resting place or retreat. Selective pressures for more efficient prey capture favored the construction of more elaborate, structured, and sticky webs.

As spiders radiated into the aerial niche they faced different selective pressures on the mechanics of prey capture. Prey immobilized on an aerial web can fall to the ground and be lost if the spider loses contact with it. Most aerial spiders wrap their prey during predation. Wrapping serves, among other functions, to sequester the prey and frees a spider from the necessity of eating its prey immediately. A further evolution in the use of prey wrapping has moved this behavior from late to earlier in an attack sequence. In situations when struggling prey could injure a spider as it approaches to bite the prey or when its struggles could allow it to escape quickly, many spiders first wrap the prey in silk to immobilize it, then approach and bite (Robinson and Robinson 1976). This method of prey immobilization is obligatory in cribellate orb-weavers of the family Uloboridae in which the poison glands are absent (Marples 1962).

Because *Scytodes* possesses several primitive morphological characteristics, yet builds an aerial web, we consider that our observations on its predatory contribute insight into possible stages in the transition from living on the ground to aerial habits.

MATERIALS AND METHODS

Spiders of a currently undescribed species in the genus *Scytodes* were collected from under picnic shelter eaves and around stones at two Texas localities: Lake Corpus Christi, San Patricio Co., and Tyler State Park, Smith Co. Voucher specimens are deposited in the American Museum of Natural History and Museo de Zoologia, Universidad de Costa Rica. The spiders were transported to Lawrence, Kansas, and housed individually in clear plastic boxes, 11 x 11 x 3 cm high, each supplied with a cotton-stoppered vial of water. The temperature was 25°C and the light cycle was irregular, but approximately L:D, 14:10. Prey were principally vestigial-winged fruit flies, *Drosophila melanogaster* (Meig.). However, cockroach nymphs (Blattaria), lacewings (Neuroptera), and small moths (Lepidoptera) were occasionally presented as well. A second generation box design employed a cork-stoppered hole through which prey were delivered singly or in groups of three to ten individuals. Subsequent predatory behavior was directly observed with (usually) two observers reporting their observations into a tape recorder. The tapes were later transcribed and the data analyzed as detailed below. After the conclusion of the sequence, the pattern of spit was observed through a binocular microscope equipped with an ocular micrometer, then sketched.

From observations of more than 70 predation attempts on a variety of prey by 15 spiders (males, females, and late juvenile instars) we developed an ethogram of the components of predatory behavior. Complete predation sequences (N = 31, 8 individuals) were then described in terms of the defined behavioral components. Durations were not recorded. The principal behaviors were serially ordered for analysis and a particular component could not follow itself in

successive acts in a sequence. The components were then put into a first-order transition matrix and transition frequencies calculated. This procedure was performed for each capture sequence of each spider. Individual results were compared and no major differences were observed between the sexes or instars. Data from all sequences were summed into one transition matrix and displayed graphically as a flow diagram.

RESULTS

Twelve behaviors comprise the ethogram of predatory behavior for *Scytodes* sp.

Alert posture.—*Structures used:* Entire body. *Action:* Space-filling posture with spider "up" on its legs. Much extension at all joints. *Context:* When walking about or just after prey contacts web lines.

Retracted posture.—*Structures used:* Entire body. *Action:* Spider appears dorsoventrally compressed in one plane. All the legs are held at the sides of the body in typical latigrade position, i.e. the femora are directed posteriorly and the more distal segments directed anteriorly. *Context:* Diurnal resting or defensive posture.

Tap.—*Structures used:* Legs I (or II). *Action:* Leg is extended, metatarsus and tarsus then flex and re-extend. Contralateral legs alternate in tapping. *Context:* Initial localization of prey after it has touched the web or spider.

Spit.—*Structures used:* Chelicerae. *Action:* Spider is in slightly elevated posture by leg extension. Spitting is accompanied by a convulsive shudder and slight posterior movement of the body. Multiple spits occasionally occur. *Context:* After prey has been contacted and is roughly positioned between extended legs I and the spider's body.

Reach and Roll (RR).—*Structures used:* Legs I (or II). *Action:* Leg is extended, then tibia, metatarsus, and tarsus are flexed and slightly retracted, then elevated and re-extended. The movement describes a circular motion with contralateral legs moving in unison. *Context:* Immediately after spitting, RR is performed distal or lateral to prey and serves to entangle it in the drying spit. It may also help to localize the prey.

Bite.—*Structures used:* Chelicerae and pedipalpi. *Action:* Pedipalpi are extended as in PALP EX. As they palpate the prey and a suitable surface is found (e.g. an appendage) the spider leans forward and bites the prey with the chelicerae. *Context:* Occurs after spitting and as the prey is cut from the spit or during wrapping.

Nibbling.—*Structures used:* Chelicerae, pedipalpi, and legs I (or II). *Action:* Distal leg segments (metatarsi or tarsi) are brought to the mouth and held there by pedipalpi. Leg is pulled out dorsally as the chelicerae nibble proximo-distally. *Context:* After RR the same legs are nibbled as were used in RR. This behavior appears homologous with nibbling seen during grooming.

Pedipalp Reciprocal Scraping (RECIP).—*Structures used:* Pedipalpi and chelicerae. *Action:* Pedipalpi scrape ipsi- or contra- lateral chelicera then scrape against one another. *Context:* Often follows nibbling and cleans dried spit from the chelicerae. It also occurs during grooming.

Pedipalp extension (PALP EX).—*Structures used:* Pedipalpi, legs I (or II), and chelicerae. *Action:* Both pedipalpi are extended with slight lateral oscillation toward a thread (dried spit or silk) held by a leg. A single pedipalp pulls the thread to the chelicerae which cut it. *Context:* Freeing the prey from the substrate by cutting the dried spit around it.

Hind leg wrap (HLW).—*Structures used:* Legs IV. *Action:* Legs alternate wiping spinnerets. Each wipe is accompanied by a lateral movement of the abdomen toward the leg which pulls silk from the spinnerets and places it around the prey which is held by legs III. *Context:* After partially or completely freeing the prey from the substrate, the prey is bound into a silk package.

Dragline attachment (DGL).—*Structures used:* Spinnerets and legs IV. *Action:* Abdomen flexed toward the surface to which attachment disc is applied. When the surface is a web line it is pulled to the spinnerets with either leg IV. *Context:* 1. Disc is applied to substrate or web line upon initial contact of prey to spider or web. 2. During wrapping, especially near completion, discs are applied to the prey package, the substrate, web lines, or several of these structures.

Feed.—*Structures used:* Chelicerae and pedipalpi. *Action:* Prey is bitten with the chelicerae and held against the mouth with the pedipalpi. *Context:* At the conclusion of the predation sequence.

Typical prey capture is similar to that reported by Monterosso (1927, 1928) for *Scytodes thoracica* (Latr.). When prey first contacts the web lines or spider's legs, the spider assumes an alert posture and usually fastens its dragline to the substrate with its abdomen or to a web thread using its abdomen occasionally aided by a leg IV. The spider then orients toward the prey and approaches it slowly, tapping with legs I, occasionally touching the prey. When the prey is approximately centered between the forelegs and the spider, it spits a net of glue at the prey (Fig. 1). The spider steps quickly to the prey; we seldom observed the leisurely saunter reported by Gertsch (1979:222). As it approaches the prey, the spider uses legs I and sometimes II in the RR motion which further entangles the prey in the rapidly drying glue. The spider infrequently spits a second time. As the spit dries on the immobilized prey, the spider palpates and bites the prey, usually on an appendage. At this point the spider alternately nibbles legs I and II with the chelicerae. This behavior is similar to nibbling of the legs observed in grooming. After nibbling, the spider begins to free the immobilized prey from the net of spit. If the prey is not securely fastened, the spider simply bites it with the chelicerae and pushes down on the substrate with all eight legs, thus pulling the prey free from the net of spit. With more securely fastened prey the spider cuts through the securing threads around the prey by drawing them to its chelicerae using the pedipalps (PALP EX) and legs I and II. Once prey is freed or has only one side attached to the substrate the spider begins to wrap the prey.

The form of scytodid hind-leg wrapping is analogous to that of araneids, theridiids, and other spiders (e.g., Robinson 1975, Eberhard 1982, for further references see DISCUSSION). The prey is held with the short legs III, while legs IV alternate in distributing loops of silk, stripped from the spinnerets, over the prey. Occasionally one leg wraps several (3-5) loops over the prey before the opposite leg is used. During wrapping the abdominal apex repeatedly waggles from side-to-side toward the leg which will apply the next loop of silk. In *Scytodes* the strands of silk are fine and we could not determine whether strands

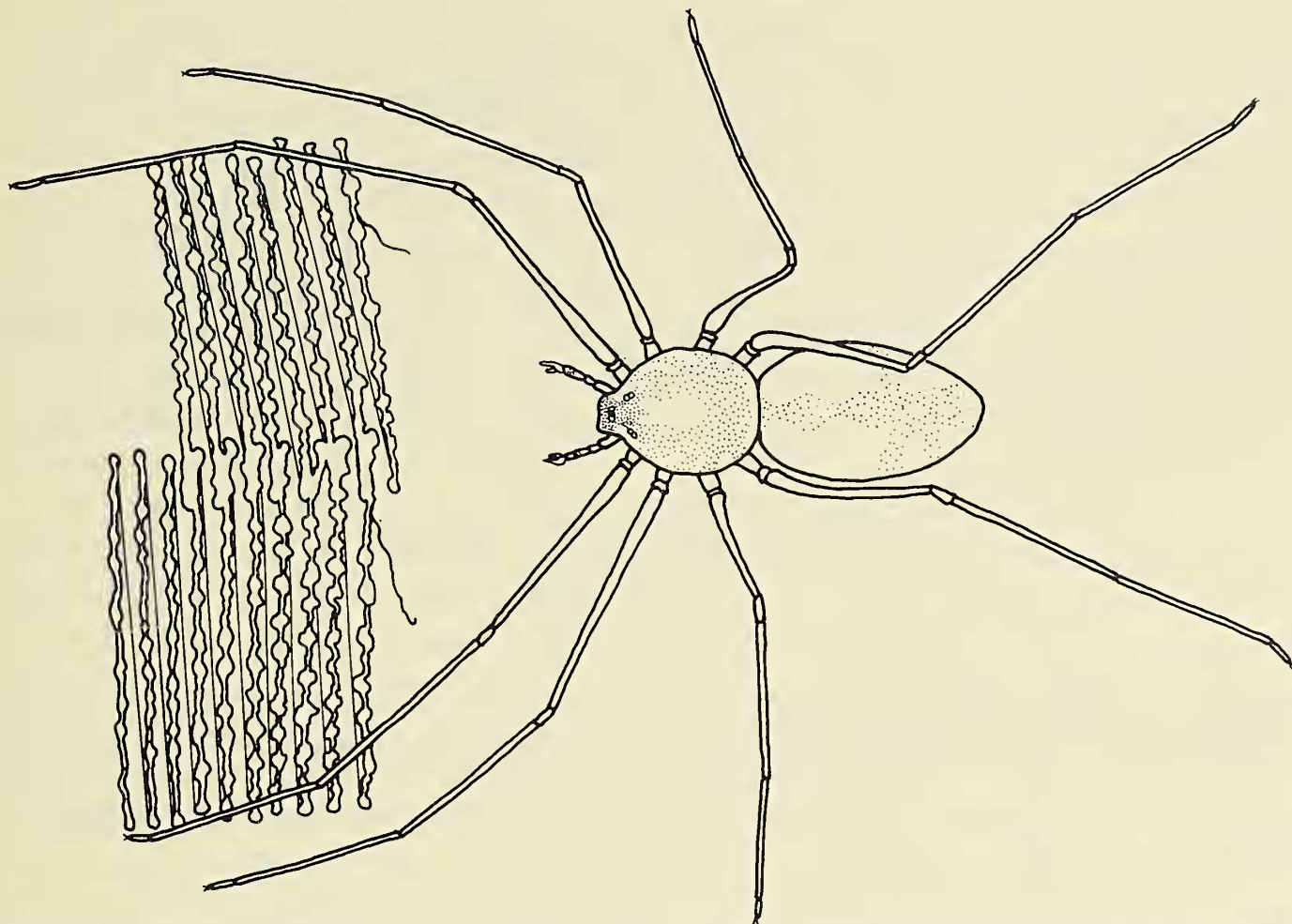


Fig. 1.—Dorsal view of *Scytodes* sp. to show the orientation of the spider and its spit immediately after spitting. Prey has been omitted for clarity.

were composed of multiple fibers. Nor could we determine from which spinnerets the silk was pulled. The strands are definitely not the swathing bands seen in *Argiope* Audouin and some other araneid genera (Robinson, Mirick and Turner 1969). The spider punctuates its wrapping by placing dragline attachment discs on the prey, the substrate, or the threads which the spider is contacting. Finally the spider holds the trussed prey in its chelicerae and begins to feed. Occasionally the spider carries the prey a short distance, but feeding generally occurs at the capture site. It is possible that the observed feeding at the capture site was an artifact of the small cages. One of us (LSR) has observed predation by *Scytodes longipes* Lucas in Costa Rica where it is found in association with human dwellings. *Scytodes longipes* typically bites its prey (in one case, a wolf spider twice its body size) and wraps it at the capture site, then carries it to its retreat before feeding.

Localization of the prey by tapping occurred prior to spitting (Fig. 2). Vision does not appear to play a role in prey localization. Prey were almost always bitten at least once before being wrapped. If prey continued to struggle, biting occurred intermittently with wrapping. A long period of feeding terminated a sequence. The sequence is not stereotyped even for the same individual capturing the same type of prey. There is variability in the number of acts per capture and in the components used. The mean number of acts per capture sequence is 19.5; the range in this study is 3 - 97. The lower bound is close to the minimum given the resolution of our component descriptions. A shorter sequence could be BITE-FEED, but this was never observed even for prey much smaller than the spider.

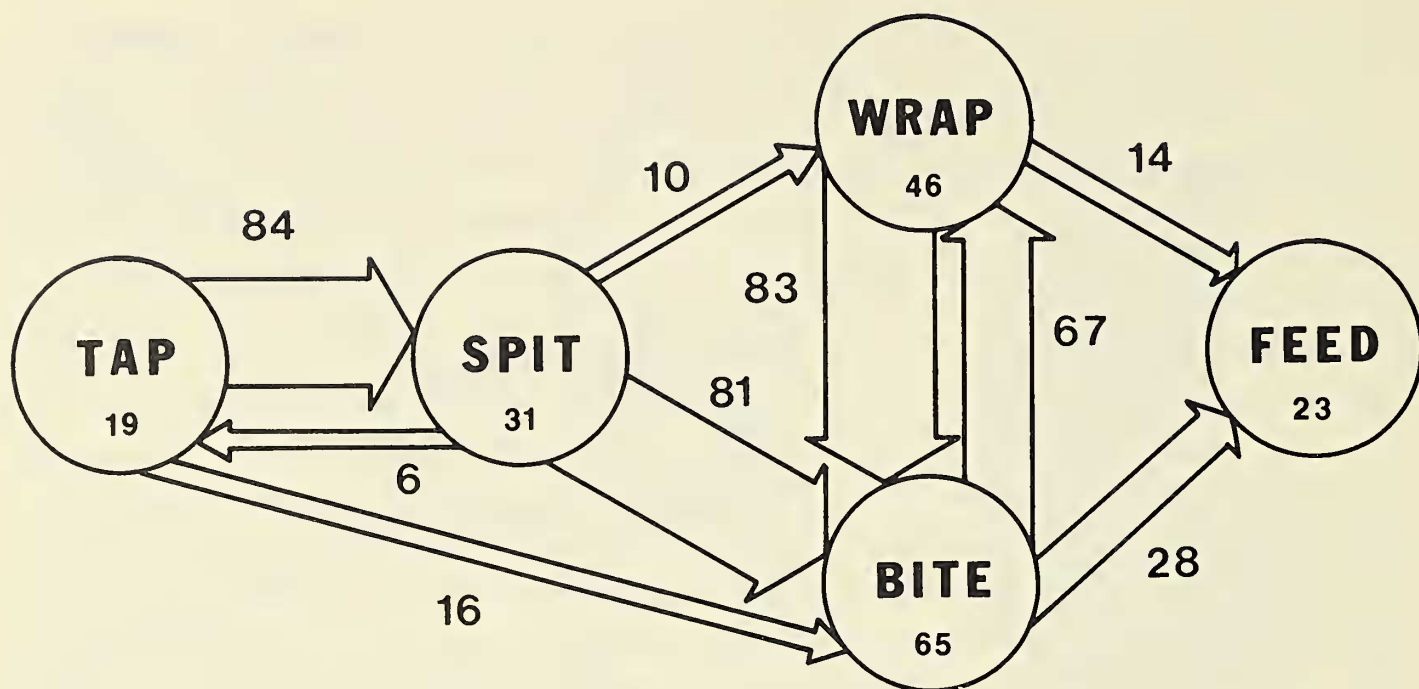


Fig. 2.—Predatory sequence of *Scytodes* sp. Main components are represented by circles; numbers within the circles are the number of occurrences of the behavior in the data set analyzed. The numbers beside the arrows and the width of the arrows represent the percentage of transitions in which a behavior was followed by the next. Transition percentages smaller than 4% have been omitted for clarity.

The upper limit may depend entirely upon the prey item. The 97 acts were used to subdue a pyralid moth 30% longer than the spider. In nature it is possible that even relatively larger prey are caught and require more acts to subdue.

Another source of variability in the predatory behavior is in the component composition of the sequence. Obviously, all the behavioral components listed in the ethogram cannot be present in a sequence of fewer acts. However, even several of the longer capture sequences did not display all behavioral components listed. We could not discern any systematic relationship between prey size and the extent of or position of wrapping in the sequence, although few large prey items were offered.

DISCUSSION

Prey capture by *Scytodes*.—Though our report of predation in this species of *Scytodes* agrees with previous general accounts, it differs significantly in one respect from the thorough study of *Scytodes thoracica* by Dabelow (1958) (see also Schaller 1956 and Kaestner 1963). The net of spit observed in *S. thoracica* reportedly consists of a single block oriented so that the parallel bands are parallel to the spiders's longitudinal axis. In the *Scytodes* sp. used in the present study, although the net itself is similar to that of *S. thoracica*, the parallel bands are perpendicular to the spider's longitudinal axis (Fig. 2). Further, the net seems always to consist of two discrete, yet often overlapping blocks of spit each composed of 5 - 17 parallel bands (mean = 10, N = 8). Typically the left and right blocks are composed of unequal numbers of bands. Similar orientations have been observed in *S. intricata* Banks (McAlister 1960), *S. venusta* (Thorell), *S. longipes* (= *marmorata* L.K.), and *S. fusca* Walkn. (= *domestica* Dol.) (Bristowe 1931).

Two other genera have recently been included in the family Scytodidae: *Drymusa* Simon and *Loxosceles* Heineken and Lowe (Gertsch 1967, but see Gertsch and Ennik 1983). *Drymusa dinora* Valerio has not been observed to use spit during prey capture (Valerio 1974). *Loxosceles* has perhaps been observed to spit, for Kaestner (1963:579) says, "*Loxosceles* Lowe, greift aus viel geringerem Abstand als *Scytodes* durch Speien von Leim aus den Cheliceren an und erzeugt dabei viel weniger regelmässig angeordnete sehr zarte Faden." However numerous other authors (Hite et al. 1966, Kaston 1972, Gertsch 1979, Foelix 1982) did not report spitting in *Loxosceles*, and this agrees with our own observations of *L. reclusa* Gertsch and Muliak and *Loxosceles* sp. made with the help of a binocular microscope.

Although the actual components of predation differ among taxa, the form of these behaviors in *Scytodes* sp. are analogous to those reported in predation of many other labidognath spiders with one exception, the component termed reach-and-roll. This maneuver, performed with both legs I and occasionally legs II serves to entangle the prey in the drying spit. Further, the spider may be applying additional fine strands of spit with its legs as it alternates between reach-and-roll and nibbling during the pre-bite portion of the sequence.

Comparative prey wrapping.—Given the present understanding of the use of silk in the predatory behavior of *Scytodes*, the remainder of the discussion will focus on the evolution of prey wrapping as an adaptation accompanying the use of aerial webs. Primitive ground-dwelling spiders, such as liphistiomorphs, do not build trapping snares and do not wrap their prey (Bristowe 1976), whereas spiders in more derived groups with aerial snares or elevated cursorial habits do exhibit prey wrapping. This difference leads to the inference that prey wrapping is an adaptive response to the increased chance of losing contact with prey in an aerial habitat.

Descriptions of the predatory behavior of "vagrant" spiders which capture prey in an elevated setting support this interpretation (Table 1). In a study of spiders of four species in the family Lycosidae, Greenquist and Rovner (1976) reported that individuals of the ground-dwelling genus *Schizocosa* Chamberlin never wrapped their prey. On the other hand, individuals of *Lycosa punctulata* Hentz and *L. rabida* Walckenaer which spend significantly more time foraging on elevated foliage exhibit post-immobilization prey wrapping at the capture site. The spider immobilizes the prey with a bite then circles it and applies silk directly from the spinnerets. We designate this as the 'primitive' prey wrapping form. This method is equally efficient on the ground or on elevated substrates. In our view, it represents a form of prey wrapping that is adaptive for above ground prey retention, not just specifically adapted to use with aerial webs. Similar forms of circular prey wrapping, occasionally involving the application of silk by legs IV, have been reported for at least one species in the following, primarily vagrant, families: Theraphosidae (M. Teeter pers. comm.), Lycosidae (Rovner and Knost 1974, Greenquist and Rovner 1976) Gnaphosidae and Hersiliidae (Bristowe 1930), Uroctiidae (Crome 1937), Oecobiidae (Glatz 1967), Psechridae (Robinson and Lubin 1979), Theridiidae (Carico 1978), and Ctenidae (Melchers 1967).

Spiders which employ aerial capture webs tend to use a second form of prey wrapping which we designate as 'derived.' The spider hangs from its web and using legs IV applies silk to the prey which may be in contact with the spider, the web, or both. This method has been reported for species in the families:

Table 1.—Summary of capture and wrapping elements of predatory behavior of spider taxa at different stages in the evolution of prey wrapping. See text for details of elements.

Taxon	Web Structure	Method of Immobilization	Wrapping Location	Wrapping Form	Feeding Location	Source
<i>Hypochilus gertschi</i> (Hypochilidae)	Aerial inverted funnel	Bite	No Wrapping		Capture site	Shear 1969
<i>Lycosa rabida</i> <i>L. punctulata</i> (Lycosidae)	Elevated capture (no web)	Bite	Capture site	Primitive	Capture site	Greenquist and Rovner 1976
<i>Fecenia angustata</i> (Psecridae)	Aerial inverted funnel/planar	Bite	Capture site	Primitive	Retreat	Robinson and Lubin 1979
<i>Diguetia albolineata</i> (Diguetidae)	Aerial inverted funnel	Bite	Retreat	Unique	Retreat	Eberhard 1974
<i>Drymusa dinora</i> (Scytodidae)	Aerial space-filling	Bite	Capture site	Primitive	Removed from capture site	Valerio 1974
<i>Scytodes</i> sp. (Scytodidae)	Aerial space-filling	Bite	Capture site	Derived	Capture site	Present study
<i>Modisimus</i> spp. (Pholcidae)	Aerial space-filling	Wrap	Capture site	Derived	Retreat	Eberhard and Briceno 1976

Diguetidae and Linyphiidae (Eberhard 1967), Theridiidae (Kaston 1965), Araneidae (Robinson 1975), Theridiosomatidae and Uloboridae (Eberhard 1982), Pholcidae (Eberhard and Briceno 1983), and Scytodidae (present study).

There is relatively little variation in the derived form of prey wrapping employed by morphologically and phylogenetically diverse taxa. This is in contrast to the enormous variation in predatory technique and to the great variation in web structure, from primitively unstructured to highly derived and secondarily reduced, in these same taxa. This similarity of form of prey wrapping, though convergent, leads us to speculate that once a taxon moves into the aerial niche there is a greater evolutionary premium associated with efficient prey handling than is associated with the actual method of prey capture or details of web structure. Thus selection has not only favored some form of prey wrapping by spiders when they capture prey above ground, but selection has tended to channelize the form of this behavior in those species well adapted to prey capture in an aerial habitat.

Examination of primitive aerial-web weavers may reflect the early steps in the evolution of prey wrapping. Predatory behavior has been described for several taxa (Table 1) in the group Filistatides (sensu Lehtinen 1967) which includes the

Hypochilomorpha and Haplogynae of other authors (Simon 1892, Petrunkevitch 1933, Platnick 1977, Brignoli 1978). The hypochilids are the most primitive taxon in this group, sharing many characters with orthognaths (Gertsch 1958, Marples 1968). *Hypochilus gertschi* Hoffmann does not wrap its prey, but merely bites the prey, pulls it through the web, and feeds at the capture site. This represents a very early stage in the evolution of aerial webs and prey wrapping.

A slightly more advanced stage may be represented by species in the cribellate family Psecridae. "The [phylogenetic] position of Psecridae is enigmatic." According to Lehtinen (1967:383) who considers them closer to his Amaurobiides than Filistatides. The family, as delimited by Forster and Wilton (1973), includes both terrestrial vagrant genera and aerial-web building genera such as *Fecenia* and *Psechrus*. *Fecenia augustata* (Thorell) immobilizes its prey by biting, then binds it to the web by applying silk directly from the spinnerets. After this primitive wrapping of the prey, it is cut from the web, carried in the chelicerae to the retreat, and eaten immediately or re-attached to the substrate.

The next stages may be represented by primitive aerial-web building haplogyne spiders. *Diguetia albolineata* (O. P.-Cambridge) (Diguetidae), also bites its prey and pulls it through the web, then transports it to the retreat where it is wrapped and eaten. The wrapping however, has a form unique to this species (Eberhard 1967:179) and may represent an independent response to the selective pressures favoring prey wrapping.

Drymusa dinora (Scytodidae) does not wrap small prey, but after immobilizing larger prey with a bite, the prey is wrapped at the capture site. The form of prey wrapping is similar to that used by *Fecenia* and spiders in "vagrant" taxa. *Drymusa* applies silk directly from the spinnerets while moving around the prey. The spider then carries it a short distance before feeding. The situation reported for *Scytodes* is different. The form of prey wrapping it uses is the typical derived form of hind-leg wrapping: alternate use of opposite legs IV in casting loops of silk over the prey.

The Pholcidae is the only other family of haplogyne aerial-web building spiders for which we are aware of detailed accounts of predatory behavior. Prey wrapping in this group is advanced both in form and in position in the predation sequence. *Modisimus* spp. wrap their prey at the capture site using the derived form. Wrapping is the first means of prey immobilization. Prey are then bitten, carried into the retreat, and eaten.

We agree with previous authors (e.g. Eberhard 1967, Robinson 1975, Lubin 1980) that the use of wrapping as the primary method of prey immobilization is the most derived use of the behavior. We suggest that because of the selective pressures on aerial prey capture, post-immobilization wrapping at the capture site was one of the earliest stages in the evolution of prey capture in aerial webs. Spider phylogeny is poorly understood and it is reasonable to assume that just as aerial webs have evolved several times (Lehtinen 1967, Kullman 1972), prey wrapping also may have evolved independently in many taxa as their members adapted to an aerial niche.

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